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Food-web structure in low- and high-dimensional trophic niche spaces

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A question central to modelling and, ultimately, managing food webs concerns the dimensionality of trophic niche space, that is, the number of independent traits relevant for determining consumer–resource links. Food-web topologies can often be interpreted by assuming resource traits to be specified by points along a line and each consumer's diet to be given by resources contained in an interval on this line. This phenomenon, called intervality, has been known for 30 years and is widely acknowledged to indicate that trophic niche space is close to one-dimensional. We show that the degrees of intervality observed in nature can be reproduced in arbitrary-dimensional trophic niche spaces, provided that the processes of evolutionary diversification and adaptation are taken into account. Contrary to expectations, intervality is least pronounced at intermediate dimensions and steadily improves towards lower- and higher-dimensional trophic niche spaces.

Keywords: intervality; evolution; Ornstein–Uhlenbeck process; Moran process; trait matching; phylogenetic correlations

1. INTRODUCTION

Elton's (1927) conception of a species' niche as 'its place in the biotic environment, its relations to food and enemies', which was later formalized by Hutchinson (1957) as a hyper-volume in a high-dimensional niche space, comprehensively relates to all ecologically relevant traits of a species. Cohen's (1977) trophic (feeding) niche space specializes this concept to traits relevant for trophic interactions. In this view, food-web links result when a resource's traits characterizing its vulnerability to predation (*resource traits*) are located within the consumer's foraging niche (Williams & Martinez 2000), characterized by its *foraging traits*.

If, for example, a species' consumers were fully determined by its mean body size, the trophic structure of a community could be represented, as in figure 1*a*, by resource body sizes and consumer foraging niches that extend across the body sizes of their resources. Standard representations of food webs, either as directed graphs with arrows pointing from resources to consumers (figure 1*b*) or as *adjacency matrices* (figure 1*c*), with the set of ones in each column indicating a consumer's diet, can then be derived. A *niche-overlap graph* (Cohen 1977; figure 1*d*) is obtained by linking two consumers if they share a common resource. This obviously implies that their foraging niches (figure 1*a*) overlap. If the niche-overlap graph of a food web can be represented by the overlaps of foraging niches given by intervals along a line, the graph is said to be *interval* (Benzer 1959) and, by extension, the food web is called interval (Cohen 1977) too. If more than one trait determines trophic interactions, that is, in higher-dimensional niche spaces, this property is not generally satisfied. Specifically, the chance that a random food web is interval becomes vanishingly small as the dimensionality of niche space increases (Cohen 1978). As a second, stronger, characterization of intervality in food webs (Critchlow & Stearns 1982; Cattin *et al.* 2004; Stouffer *et al.* 2005), a web's adjacency matrix web is said to have the *consecutive-ones property* (COP) along the columns, if, with an appropriate ordering of species, the ones in each column are consecutive (figures 1*c* and 2*a*). (For examples of food webs that are interval but do not have the COP, see fig. 2*c* of Cattin *et al.* (2004) or our figure 2*a*.) A third, weaker, characterization of intervality used in some studies (Sugihara 1982; Huxham *et al.* 1996; Cattin *et al.* 2004) is the *chordal* property[1] of the niche-overlap graph (essentially, graphs are chordal if each minimal cycle is a triangle; figure 1*d*). Niche-overlap graphs are chordal if they are interval, but the reverse is not always true (Golumbic 1980).

The surprisingly high frequency of interval webs in empirical data (Cohen 1978) has been interpreted as an indication of an approximately one-dimensional trophic niche space. This interpretation of intervality is, for example, documented in the work by Cohen (1977): 'Why One Dimension?'; Williams & Martinez (2000): 'Our results show that, with respect to food-web structure, community niche space is usefully

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[1]If no pair of vertices that are non-adjacent in a cycle of a graph are connected by a link, the cycle is called *chordless*. A graph is called *chordal* if it has no chordless cycles of length larger than three.

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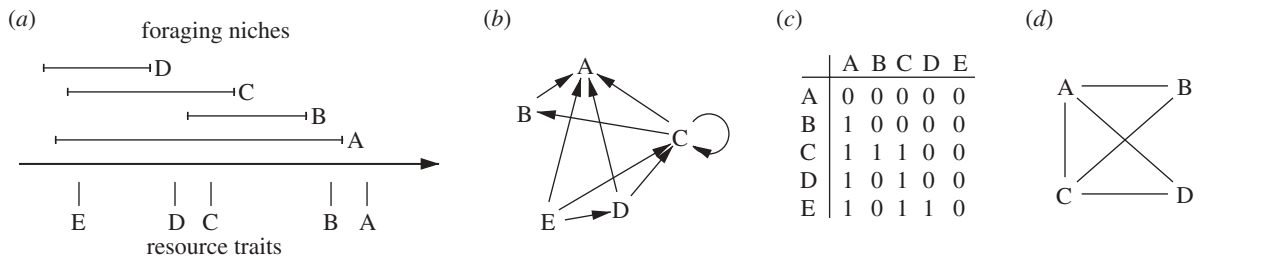

Figure 1. Representations of food webs. (*a*) Resource traits and foraging niches in a one-dimensional niche space. (*b*) Food-web graph displaying the resulting resource–consumer links. (*c*) Adjacency matrix of the food-web graph. (*d*) Niche-overlap graph indicating which consumers share resources.

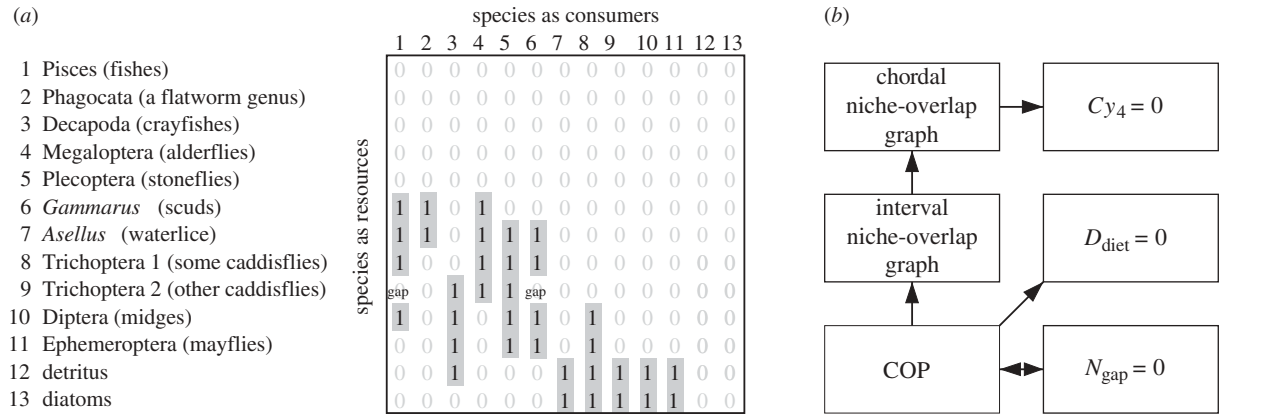

Figure 2. The COP and related food-web characteristics. (*a*) Adjacency matrix of the food web 'Morgan's Creek' (Minshall 1967; Cohen 1978). Indices of columns and rows refer to the same food-web vertices. Each '1' in the matrix specifies a diet item of a consumer. The label 'gap' indicates additional diet items that would need to be added to give the matrix the COP along the columns. The presence or absence of the gaps here does not affect the niche-overlap graph. This food web is therefore interval even though it violates the COP. (*b*) Logical relations between qualitative characterizations of intervality (see §1) and related quantitative measures (see §2.5). Arrows indicate logical implications. The COP, explained by our theory, implies intervality by all other criteria.

collapsible to one dimension'. Stouffer *et al.* (2006): 'Importantly, the degree of intervality of a food web is related to the number of trophic dimensions [...] If a food web is interval, then the species and their diets can be represented along a single dimension'. Mouillot *et al.* (2008): 'In an interval host-parasite web [...] a single dimension and thus a single niche axis (for instance host body size) is enough to structure host-parasite relationships' and in fig. 2 of Allesina *et al.* (2008). Several candidates for the trait corresponding to this dimension, most prominently body size (Lawton & Warren 1988), have been considered (Cohen 1978), but difficulties in establishing the association persist (Cohen 1978; Stouffer *et al.* 2006). Yet, food webs are now regularly modelled as essentially structured by body size or some abstract trait variable (Williams & Martinez 2000; Camacho *et al.* 2002; Loeuille & Loreau 2005; Stouffer *et al.* 2006; Camacho *et al.* 2007; Lewis & Law 2007; Allesina *et al.* 2008; Guill & Drossel 2008; Petchey *et al.* 2008), which may also have contributed to identifying community size structure as an ecological management objective (ICES 2006). An alternative view, proposed by Sugihara (1982, 1984) argues that even in high-dimensional niche spaces a specific community assembly rule (perfect addition ordering, Sugihara 1984) naturally enforces chordal niche-overlap graphs and that this constraint is sufficient to produce the observed frequency of interval graphs in nature. Specific empirical tests of the postulated assembly rule would therefore be of high interest. Others have argued that evolutionary processes might cause intervality (Sugihara 1982; Williams & Martinez 2000; Cattin *et al.* 2004; Rossberg *et al.* 2006*b*; Mouillot *et al.* 2008). In fact, phylogenetic correlations in food webs are known to be strong (Cattin *et al.* 2004) and underlie the common practice of aggregating larger taxonomic groups in food webs to single compartments (e.g. figure 2*a*). A prominent interpretation of food-web structure (Cattin *et al.* 2004) invokes the tendency of phylogenetically related consumers to share resources as the structuring mechanism, thereby interpreting Sugihara's assembly rule on an evolutionary time scale.

The purpose of our study here is to develop a coherent, quantitative and unified theory of intervality, accounting for the combined effects of niche-space dimensionality and phylogenetic correlations, their relative strengths and potential synergies. In contrast to previous work that drew on the tendency of phylogenetically related consumers to share resources (Sugihara 1982; Cattin *et al.* 2004), our theory relies on the tendency of related resources to share consumers, i.e. on phylogenetic correlations between resource traits, which appear to be even stronger than those between foraging traits (Blomberg *et al.* 2003; Rossberg *et al.* 2006*a*; Bersier & Kehrli 2008).

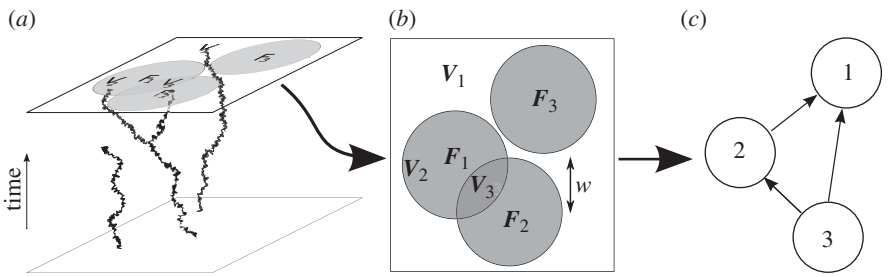

Figure 3. Illustration of the model. (*a*) Resource traits $\boldsymbol{V}_i$ of species evolve through branching random walks, here in a two-dimensional trophic niche space. At each branching event (in variants II and III), a third species is removed. The evolution of foraging traits $\boldsymbol{F}_i$, thought to be much faster, is not modelled on this time scale. (*b*) Trophic links result if resource traits of resources fall within the foraging niches of consumers, given by circles in niche space with radius w around foraging traits. In variants I and II, the locations of foraging traits in niche space are identified with those of randomly chosen resource traits, and in variant III, they are dynamically adapted. (To avoid visual clutter, resource and foraging traits are chosen independently in (*b*)). (*c*) The resulting food web.

2. MATERIAL AND METHODS

2.1. General model structure

To gain better insights into the relationships between niche-space dimensionality, phylogenetic correlations and intervality, we developed three successive variants of an evolutionary food-web model. In all variants, each species is characterized by two separate sets of resource and foraging traits. The model couples minimal sub-models for the following three aspects of ecology: how trophic interactions are determined by resource and foraging traits (emphasizing the notion of trophic niches), how the resource traits of the species comprising a community are determined (emphasizing the role of evolutionary diversification) and how the foraging traits of these species are determined (emphasizing the role of evolutionary adaptation). The number of relevant resource traits and foraging traits per species, that is, the dimensionality D of trophic niche space, is treated as a model parameter.

2.2. Determination of trophic links from trophic traits

We studied model food webs (figure 3) resulting from interactions between a fixed number S of species. Associated with each species i is a D-dimensional vector representing abstract resource (or vulnerability) traits $\boldsymbol{V}_i$ and another D-dimensional vector representing abstract foraging traits $\boldsymbol{F}_i$ (for a detailed motivation, see Rossberg *et al.* 2010). Species i consumes species j if the distance $|\boldsymbol{F}_i - \boldsymbol{V}_j|$ between $\boldsymbol{F}_i$ and $\boldsymbol{V}_j$ is smaller than some fixed trophic niche width w (figure 3*b*,*c*). Since our purpose here is to demonstrate a general mechanism rather than reproducing specific empirical data, complicating assumptions such as a trophic hierarchy or a distinction between consumers and producers were not included in the model. These are not essential for our arguments and conclusions, as we shall explain below. We set the number of species to $S = 50$. For each model variant and niche-space dimensionality, the niche width w was always chosen such that the expected number of trophic links per species was 10 (see appendix B). These are typical values for recently published empirical food-web data sets (Dunne *et al.* 2002).

2.3. Determination of resource traits

In the first model variant (I), we assume that the resource traits of each species i evolve independently through mean-reverting random walks (D-dimensional Ornstein–Uhlenbeck (OU) processes; Felsenstein 1988; Blomberg *et al.* 2003)

$$\mathrm{d}\boldsymbol{V}_i(t) = -r\,\boldsymbol{V}_i(t)\,\mathrm{d}t + \boldsymbol{\sigma}\,\mathrm{d}\boldsymbol{W}_i. \tag{2.1}$$

The reversion rate r characterizes the evolving tendency of traits to return to a set of environmentally and physiologically preferred values, located at $\boldsymbol{V}_i = 0$ by our choice of coordinates. This tendency is counteracted by other, species-specific evolutionary drivers on resource traits, resulting, for example, from trophic and non-trophic interactions with other species or from environmental variation. We assume that these drivers vary on time scales that are short compared to the time scale of community-level macroevolution. Across macroecological times, they can therefore be approximated as random noise (Felsenstein 1988; Blomberg *et al.* 2003; Pie & Weitz 2005). These drivers are represented by the second term on the right-hand side of equation (2.1). The differential $\mathrm{d}\boldsymbol{W}_i$ (where $\boldsymbol{W}_i$ denotes a D-dimensional Wiener process) is the mathematical representation of D independent 'noise' variables of unit strength, and the parameter $\boldsymbol{\sigma}$ scales the resulting rate of evolutionary drift (Felsenstein 1988; Blomberg *et al.* 2003). In this first model variant, there are no phylogenetic correlations between the resource traits of coexisting species.

In the other two model variants (II and III), the resource traits of each species still evolve through a mean-reverting random walk, but phylogenetic correlations among them are generated by random branching events occurring at a rate s per species. These model evolutionary diversification through the speciation of a species, by adding an identical copy of it to the system (figure 3*a*). The shorter the time since the separation of two species, the closer their resource traits in niche space are going to be. Competitive exclusion limits the number of species that can co-exist in a community. Thus, with each new species introduced, another one will locally become extinct on the average (Drossel *et al.* 2001). We model this effect here by randomly removing, at each speciation event,

one other species, so that the total number of species S in the food web remains constant (Moran process). We choose units of time and distance in niche space such that $s = \boldsymbol{\sigma} = 1$ without loss of generality. Then r^{-1} corresponds to the time over which a species 'remembers' its phylogenetic origin in units of speciation times. We set $r = 0.01$ to reflect the observed pattern of largely divergent, but occasionally convergent, evolution. (In model variant I, any value of $r > 0$ has the same effect on results.) A special algorithm (appendix A) allowed us to sample the resource traits for all model variants from the exact stochastic steady state of resource-trait evolution. The steady state does not depend on initial conditions.

2.4. Determination of foraging traits

Empirical observations indicate that foraging traits evolve considerably faster than resource traits and that phylogenetic correlations among foraging traits are weak (Blomberg *et al.* 2003; Rossberg *et al.* 2006*a*; Bersier & Kehrli 2008). For example, Cooper & Vitt (2002) documented several independent transitions between carnivory and omnivory/herbivory within families of lizards, that is, within clades much smaller than the full evolutionary tree spanning the biome of a typical food web. Phylogenetic correlations among foraging traits are therefore not included in the model. Instead, we assume foraging traits to be determined through evolutionary adaptation to resources on a short time scale. As a simple way of modelling such a fast adaptation of foraging traits to resource traits in model variants I and II, we assume that each species has optimized its foraging traits to one particular resource. Thus, technically, after sampling resource traits, we choose for each species i a random resource j (with replacement), set $\boldsymbol{F}_i = \boldsymbol{V}_j$, and say that i is *focused* on j.

In model variant III, foraging traits $\boldsymbol{F}_i$ are determined by modelling, in a simplified form, the tendency of consumers to dynamically adapt such as to increase their fitness. The fitness f_j of each species j combines positive effects from adaptation to resources with negative effects from interference competition with consumers with similar foraging traits (Loeuille & Loreau 2005). These two effects are described by the first and second term, respectively, in our model for f_j

$$f_j = \sum_i \exp\left(-\frac{|\boldsymbol{V}_i - \boldsymbol{F}_j|^2}{2w_V^2}\right) - a\sum_i \exp\left(-\frac{|\boldsymbol{F}_i - \boldsymbol{F}_j|^2}{2w_F^2}\right). \tag{2.2}$$

Parameters a and w_F are chosen to describe weak interference competition ($a = 0.2$) over a narrow range in niche space ($w_F = w/6$, where w is the niche width used for model variant II); we set $w_V = w/3$, to interpret the niche width w as the cut-off radius at which the trophic interaction strength drops to $\exp(-(1/2)w^2/w_V^2) \approx 1\%$ of its maximum. The adapted foraging traits in model variant III are obtained, starting from model variant II, by letting foraging traits evolve along the directions of the steepest fitness gradients ($\mathrm{d}\boldsymbol{F}_j/\mathrm{d}t = \partial f_j/\partial \boldsymbol{F}_j$) until a fixed point is reached.

To summarize, model variant I describes uncorrelated resource traits and focused foraging traits, variant II describes correlated resource traits and focused foraging traits and variant III describes correlated resource traits and adapted foraging traits.

2.5. Measures of intervality

To quantify intervality in the resultant food webs, we determined the probabilities P_{COP}, P_{interval} and P_{chordal} of obtaining food webs with the COP or with interval or chordal niche-overlap graphs, respectively, and also computed model averages of the following three quantitative measures of intervality used in the literature: the minimum number N_{gap} of additional links ('gaps', figure 2*a*) required to obtain the COP (Stouffer *et al.* 2006), the fraction D_{diet} of triplets of consumers with more than one resource that do not have the COP (Cattin *et al.* 2004) and the number Cy_4 of cycles of length four in the niche-overlap graph that violate the chordal property (Huxham *et al.* 1996; Cattin *et al.* 2004). Logical relations (Critchlow & Stearns 1982; Sugihara 1982; Cattin *et al.* 2004; Stouffer *et al.* 2006) between these characterizations of intervality are illustrated in figure 2*b*.

3. RESULTS

We analysed trophic niche spaces with $D = 1$ to $D = 20$ dimensions, as well as with $D = 200$ and $D = 2000$. Naturally, all model variants exhibited perfect intervality for a one-dimensional niche space. In the absence of phylogenetic correlations (variant I, dotted lines in figure 4), deviations from intervality rapidly increased with D and remained large for D up to 2000. Deviations in terms of niche-overlap graphs ($1 - P_{\mathrm{interval}}$, $1 - P_{\mathrm{chordal}}$, Cy_4) slightly decreased with increasing D, but the three measures based directly on the adjacency matrix ($1 - P_{\mathrm{COP}}$, D_{diet}, N_{gap}) increased monotonically. These results correspond to the standard interpretation (Cohen 1977) of intervality as being indicative of $D \approx 1$. By contrast, with phylogenetic correlations (variant II, continuous lines), deviations from intervality were maximal at $D = 2$ or $D = 3$ and then decreased with increasing D, approaching perfect intervality for large D. Adaptation of foraging traits (variant III, dashed lines) enhanced intervality further. (As a result of this adaptation, the average number of links per species increased slightly to between 11 and 13. By increasing the niche width w and thus the number of links per species, we easily verified that this increase alone would worsen intervality, rather than improving it.)

4. DISCUSSION

4.1. Mechanism for intervality in high dimensions

The concept of trophic niche space implies that a consumer's diet consists of those species whose resource traits fall into its foraging niche. Hence, a consumer's

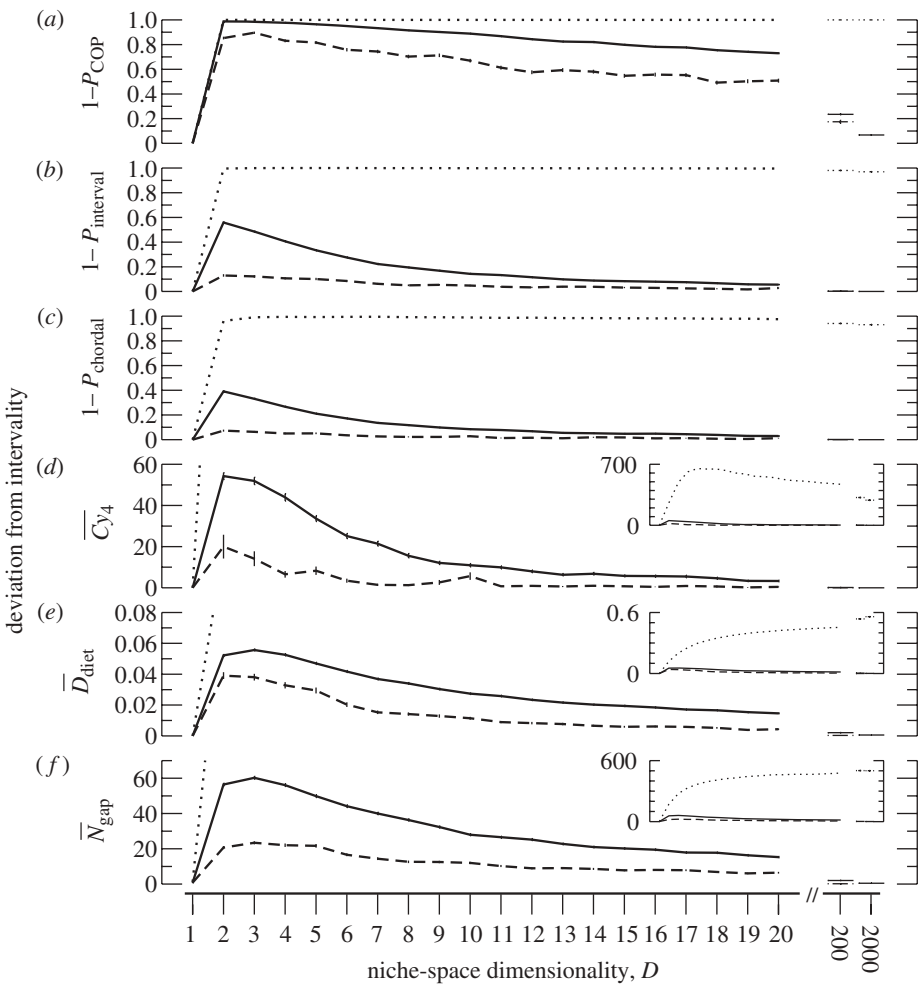

Figure 4. Deviations from perfect intervality in dependence on niche-space dimensionality, D. (*a*) P_{COP}, (*b*) $P_{interval}$ and (*c*) $P_{chordal}$ denote the probabilities of obtaining food webs with COP and webs with interval and chordal niche-overlap graphs, respectively. (*d*) $\overline{Cy}_4$, (*e*) $\overline{D}_{diet}$ and (*f*) $\overline{N}_{gap}$ denote the averages of the quantitative measures for deviations from intervality explained in the text. Dotted lines (model variant I) and continuous lines (variant II) correspond to focused consumers without and with phylogenetic correlations, respectively (10 000 sample webs per point; for $\overline{N}_{gap}$ only 1000 for computational reasons; see Stouffer *et al.* 2005), dashed lines correspond to adapted consumers (variant III; 1000 sample webs per point, $D = 2000$ excluded for computational reasons). Insets expand vertical axes. Vertical bars, where visible, indicate s.e.

diet items are similar in terms of their resource traits. Related species are generally more similar to each other than unrelated ones. As a result, consumers tend to forage on closely related species. They could therefore be said to perform a cladistic analysis through their foraging behaviour. From the practice of cladistics, it is well known that such an analysis, though sometimes difficult and prone to errors in details, tends to become more accurate the larger the number of traits that are included. By analogy, we expect the cladistic coherence of resource sets of consumers to increase with the number of resource traits. The ideal situation in which resource sets are identical with branches of the phylogenetic tree immediately implies food-web intervality (figure 5). As we argue in the following, this ideal situation is in fact approached by our model in the variants with phylogenetic correlations as the number of resource traits, i.e. the dimensionality of trophic niche space, increases. Two aspects of the model are important here, and both can be expected to persist in more detailed descriptions of food webs.

First, the squared distance between the resource traits of two species is, by definition, the sum of the squared distances in each of the D dimensions. The distance in each dimension (i.e. for each trophic trait) is a random variable and in general hard to predict. But if D is large, the sum of the squared distances will, nevertheless, approach a well-defined value (by virtue of the central limit theorem). Specifically, the coefficient of variation, CV, of the squared distance decreases with D as $1/D^{1/2}$. In our model, distance squared follows, up to a constant factor, a χ^2-distribution with D degrees of freedom (see appendix B). This implies $\mathrm{CV} = (2/D)^{1/2}$.

Second, by the assumed random nature of resource-trait evolution, the mean (or expected) squared distance between the resource-trait vectors $\boldsymbol{V}_i$ of two species increases, in model variants II and III, with the time since separation of their lineages (for a derivation of the precise relation, see appendix B).

Taken together, these two points imply that, for sufficiently high D, the distance between resource traits of two species in model variants II and III is determined

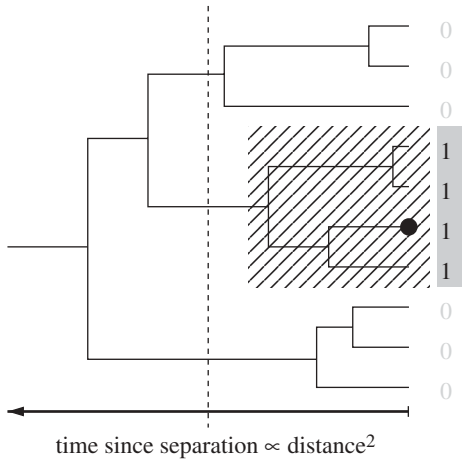

Figure 5. Phylogenetic explanation of intervality. Our model implies that for high-dimensional niche spaces the distance between the resource traits of two species strictly increases with the time since separation of their lineages (tree diagram). The diet of a focused consumer is given by all species with resource traits closer than some niche width to its focal species (filled circle), that is, by those lineages that separated from the focal species less than a given time ago (dashed line). This diet set corresponds to a branch (hatched area) of the phylogenetic tree and to a set of consecutive ones along the tree's tips.

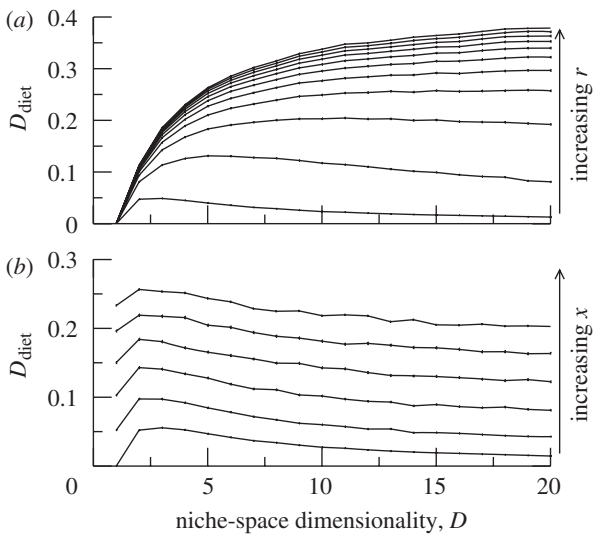

Figure 6. Intervality in non-ideal model food webs. Intervality is weakened and thus D_{diet} is raised, by (*a*) increasing the reversion rate r ($r = 0, 0.1, \ldots, 1$ in units of the speciation rate) and also by (*b*) randomly rewiring a fraction x of a food web's trophic links ($x = 0, 0.02, \ldots, 0.1$). Model variant II with remaining parameters as in figure 4. All lines in (*a*) approach 0 for sufficiently high D (not shown).

by the time since the separation of their lineages: the larger this time, the more their resource traits are separated. As explained in figure 5 for model variant II, this implies that diet sets correspond to branches of the phylogenetic tree, which, in turn, implies intervality. This explanation would apply equally to model variants in which (IV) some species (producers) do not forage, (V) niche width varies between consumers, (VI) body size affects the selection of a consumer's focal resource or where (VII) a trophic hierarchy constrains consumer–resource interactions. Our findings therefore apply to a wide class of models.

The effect of dynamic adaptation in variant III to further enhance intervality (figure 4) can also be understood. Seeking to increase its fitness, a consumer will typically adapt its foraging traits $\boldsymbol{F}_i$ so as to centre them within the cluster of the resource traits of its prey: this improves the correspondence between resource sets and branches of the phylogenetic tree in comparison to the case with focused consumers, which, in turn, enhances intervality.

4.2. Weaker intervality in empirical data

Large empirical food webs typically exhibit less pronounced intervality than that shown in figure 4 (Cohen *et al.* 1990; Cattin *et al.* 2004; Stouffer *et al.* 2006). For example, Cattin *et al.* (2004) found values of D_{diet} ranging from 0.004 to 0.35, with a mean of 0.18, for a collection of seven food webs ranging in size from $S = 25$ to 94, while we found at most $D_{\mathrm{diet}} = 0.056$ for the model variants with phylogenetic correlations (II and III). The same study reports empirical values for Cy_4 between 0 and 639 with a mean of 158, while mean Cy_4 in figure 4 reaches at most 54 with phylogenetic correlations. Stouffer *et al.* (2006) report, for an extension of this collection to 15 food webs, values of N_{gap} between 1 and 700 with an average of 223 (or 126 when constraining to the seven webs of Cattin *et al.* (2004)), while the maximum average value reached for N_{gap} in figure 4 with phylogenetic correlations is 60. Our model was neither designed to quantitatively reproduce empirical food webs, nor does this comparison account for differences in food-web size and link density between data sets. Nevertheless, one might interpret these figures as indicating a general trend towards less pronounced intervality in empirical data than in our model.

It is therefore important to highlight that, when relaxing idealizations of our model, intervality is readily brought into alignment with reported empirical values. For example, when increasing in model variant II the tendency of resource traits to revert to the origin (r), so as to reduce phylogenetic correlations (Blomberg *et al.* 2003), the maximum of D_{diet} shifts to increasingly larger dimensions D (see, e.g., figure 6*a*). For smaller D, the value of D_{diet} then approaches the uncorrelated case. As another example, to account for aspects of evolution and ecology not captured by our simple model (e.g. homoplasies, uneven rates of evolution or complex geometries of trophic niches), we randomly removed a fraction x of the trophic links in food webs generated by model variant II and randomly added the same number of links at other positions, thus generating webs with small-world topologies. With only 10 per cent of links rewired, D_{diet} again reaches typical empirical values (see, e.g., figure 6*b*). The same trends are observed for other measures of intervality (not shown). Since intervality implies a highly specific food-web topology, most variations of topology tend to destroy it. We propose that this strong sensitivity of quantitative departures from intervality ought to caution against deducing niche-space dimensionality from intervality alone.

4.3. Conclusions and outlook

We have shown that food-web topology does not exclude high-dimensional trophic niche spaces, once the evolutionary processes of diversification and adaptation are taken into account. It is therefore quite possible that many independent traits of consumers and resources together determine trophic links in natural communities. Sibbing & Nagelkerke (2001), for example, identified several traits of barbs and their resources that potentially affect feeding relations. Resources might, for example, be selected by their habitat, size, swimming velocity, shape, mechanical properties and chemical composition. Barbs, on the other hand, differ in their characteristics related to search and detection of food, speed and duration of swimming, suction, filter feeding, biting and scraping, prey selection by size and taste and digestion, among others. It therefore seems evident that new approaches are required to assess the dimensionality of trophic niche spaces. A method that could be useful for this purpose has recently been introduced by the authors (Rossberg *et al.* 2010).

Phylogenetic clustering through evolutionary diversification and adaptation plays a central role in our analysis. Such clustering might also explain other properties of food webs, such as the apparent block structure of adjacency matrices (Critchlow & Stearns 1982; Allesina & Pascual 2009), the abundance of specific network motifs (Stouffer *et al.* 2007), the absence of holes in resource graphs (Sugihara 1982) and the particular distribution of the number of a consumer's resources (Camacho *et al.* 2002; see the arguments by Rossberg *et al.* (2006*b*) and Laird & Jensen (2006)). When intervality is no longer interpreted as constraining the dimensionality of trophic niche space, the potential of evolutionary processes for structuring communities is re-asserted.

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APPENDIX A

Here, we show how exact steady-state samples of our food-web model are computed without having to simulate the underlying stochastic dynamics. First, we recall that for a one-dimensional OU process

$$\mathrm{d}x = -r\,x\,\mathrm{d}t + \boldsymbol{\sigma}\,\mathrm{d}W, \tag{A 1}$$

the variance at $t=0$ for a process x starting from a deterministic initial condition at $t=-T$ is

$$\operatorname{var} x|_{t=0} = \frac{\boldsymbol{\sigma}^2}{2r}\,[1-\exp(-2\,r\,T)]. \tag{A 2}$$

We denote by $V_k(i)$ the ith component ($1 \le i \le D$) of the vulnerability vector $\boldsymbol{V}_k$ of species k at $t=0$. By the linearity of the OU process and equation (A 2), we obtain for model variants II and III (which include phylogenetic correlations)

$$\operatorname{var}(V_k^{(i)} - V_l^{(i)}) = \frac{\boldsymbol{\sigma}^2}{r}\,[1-\exp(-2\,r\,T_{kl})], \tag{A 3}$$

where T_{kl} is the time since separation of the lineages of k and l. We define the function relating times T to variances v as

$$v(T) := \frac{\boldsymbol{\sigma}^2}{r}\,[1-\exp(-2\,r\,T)]. \tag{A 4}$$

Model variant I (which excludes phylogenetic correlations) corresponds to the limit $T \to \infty$, $v(T) \to \boldsymbol{\sigma}^2/r$.

Now, we choose an arbitrary species m as a reference point. In order to obtain the covariance matrix of the vulnerability vectors of the other species relative to m, we observe that

$$\begin{aligned}\operatorname{var}(V_k^{(i)} - V_l^{(i)}) &= \operatorname{var}\Big[(V_k^{(i)} - V_m^{(i)}) - (V_l^{(i)} - V_m^{(i)})\Big]\\ &= \operatorname{var}(V_k^{(i)} - V_m^{(i)})\\ &\quad - 2\operatorname{cov}(V_k^{(i)} - V_m^{(i)}, V_l^{(i)} - V_m^{(i)})\\ &\quad + \operatorname{var}(V_l^{(i)} - V_m^{(i)}).\end{aligned} \tag{A 5}$$

Thus

$$\begin{aligned}&\operatorname{cov}(V_k^{(i)} - V_m^{(i)}, V_l^{(i)} - V_m^{(i)})\\ &= \frac{v(T_{km}) + v(T_{lm}) - v(T_{kl})}{2},\end{aligned} \tag{A 6}$$

which can be evaluated using equation (A 4), provided the phylogenetic matrix (T_{kl}) is given. Since the solutions of the OU equation are normally distributed, the covariance fully determines the distribution of the resource traits relative to $\boldsymbol{V}_m$. The standard method for drawing samples from this distribution is to multiply the lower triangular factor of the Cholesky decomposition of the covariance matrix with a vector of independent standard normally distributed random numbers. The focused foraging traits are obtained by randomly drawing from the set of S species, with replacement, for each consumer one species as its focal species.

Phylogenetic matrices (T_{kl}), or coalescence times, of Moran processes can be sampled efficiently by simulating the coalescence of the S lineages backwards in time until all lineages are connected (Hein *et al.* 2005). Since speciation events are assumed to occur spontaneously and independently, the Gillespie algorithm (Gillespie 1977) can be used: times between subsequent coalescence events are drawn from an exponential

distribution with mean τ given by

$$\tau^{-1} = s\,M\,\frac{M-1}{S-1}, \tag{A 7}$$

where s is the speciation rate and M is the number of lineages remaining to be connected. To understand equation (A 7), it is useful to randomly label the two species emerging from a speciation as ancestral and child species. The probability for a species to coalesce with any child species going backwards in time by a short step Δt is $s\Delta t$, the probability for any of the M unconnected species to do so is $s\,M\,\Delta t$, accounting for the first two factors in equation (A 7). The last factor in equation (A 7) represents the probability that the child species is from one of the other $M-1$ unconnected lineages present at $t=0$, rather than from a lineage that dies out before $t=0$.

APPENDIX B

An analytic expression for the expectation value $\mathsf{E}(Z_c)$ of the number Z_c of links per consumer for model variants I and II is derived. This result allowed us to adjust the trophic niche width w depending on the number of trophic niche-space dimensions D such as to obtain a specified value for $\mathsf{E}(Z_c)$.

First, notice that in model variants I and II each consumer has one focal resource species l to which it is linked. The probability that a consumer has any other species k as its resource is the probability that $|\boldsymbol{V}_k - \boldsymbol{V}_l|^2 < w^2$. Since the differences between vulnerabilities are normally distributed, $|\boldsymbol{V}_k - \boldsymbol{V}_l|^2$ is distributed as $v(T_{kl})\chi^2_D$, with v as defined in equation (A 3) and the last factor following a χ^2-distribution with D degrees of freedom. (This implies that the expected squared distance between two vulnerability trait vectors equals $v(T_{kl})D$ and, as required in §4.1, increases with increasing T_{kl}.) The probability of linking a consumer focused on l to a resource $k \neq l$, given the coalescence time T, is given by the cumulative χ^2-distribution

$$p(T) = \frac{\gamma(D/2, w^2/(2\,v(T)))}{\Gamma(D/2)}, \tag{B 1}$$

where $\gamma(x,y) = \int_0^y \mathrm{e}^{-t}\ t^{x-1}\ \mathrm{d}t$ is the incomplete γ function and $\Gamma(x) = \gamma(x,\infty)$ the standard Γ function.

For model variant II, the coalescence time has an exponential distribution with mean (Hein *et al.* 2005) $\tau_c = (S-1)/2s$, i.e. the value of τ given equation (A7) with $M=2$. The probability for a consumer focused on l to forage also on $k \neq l$ can thus be obtained as

$$P_{\mathrm{link}} = \frac{1}{\tau_c}\int_0^\infty \exp(-T/\tau_c)p(T)\mathrm{d}T. \tag{B 2}$$

This integral needs to be evaluated numerically. For model variant I, we obtain $P_{\mathrm{link}} = \lim_{T\to\infty} p(T)$. For both variants I and II, the expected number of links per consumer is given by

$$\mathsf{E}(Z_c) = 1 + (S-1)P_{\mathrm{link}}. \tag{B 3}$$

We numerically solved this equation for w to obtain the niche width that yields the desired expected number of links per consumer.

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